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Modelling the dynamics of oak-pine Mediterranean forests in a climate change scenario

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The role of the student in this thesis consisted of:

- Selecting and processing data from the IEFC database. Entirely done by the student.
- Processing climate data and generating climate series with ForClim. Done by the student with the assistance of Raúl García Valdés.
- Simulating forest growth with ForClim and processing the results. Entirely done by the student.
- Running statistical analyses of the results and interpreting them. Done by the student with the assistance of Jordi Martínez-Vilalta and Raúl García Valdés.
- Writing the final manuscript. Entirely done by the student.

This thesis is written following the author guidelines of Global Change Biology.

Modelling the dynamics of oak-pine Mediterranean forests in a climate change scenario

Running head:

CLIMATE CHANGE IMPACT ON FOREST DYNAMICS

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Abstract

Climate change is affecting forest communities all around the globe. Increased aridity due to warmer temperatures is causing widespread cases of drought-induced forest dieback, thus altering forest dynamics. This is particularly noticeable in dry areas, such as the Mediterranean, where many species are found at the dry edge of their distribution. In this study we use a forest succession model, ForClim, to bring some insight into how two currently dominant species (*Pinus sylv*estris and *Quercus humilis*) will behave under the expected climate change in Catalonia, NE Spain, where they currently coexist. We found a generalized decrease in biomass and productivity for both species, both in monospecific and mixed stands, with the only exception of *Q. humilis* in mixed stands. Such decrease was not homogeneous between species. Contrary to most experimental evidence from our study area, we found a greater decrease of *Q. humilis* than *P. sylvestris* in monospecific stands, while the opposite was observed in mixed stands. Such disparity may be a consequence of the interspecific competition modulating the effects of climate change, although the modeling exercise we performed has important limitations that have to be taken into account. Ultimately, this study reveals the difficulty of modeling species behavior in rear edge populations, thus highlighting the importance of further studying and understanding these populations.

Introduction

Temperature rise caused by climate change has been associated to increased number of drought-induced forest diebacks (van Mantgem *et al.*, 2009, Allen *et al.*, 2010, Carnicer et al., 2011, Allen *et al.*, 2015). Shifts in climatic conditions have also lead to changes in tree growth, affecting forest characteristics and functions, such as biomass storage, wood productivity and resilience to disturbances (Schröter *et al.*, 2005, McDowell *et al.*, 2008, Vilà-Cabrera *et al.*, 2012). Ultimately, such changes in the environmental conditions may modify forests community composition (Granda *et al.*, 2013), in some cases reducing the number of species present in the community (Thuiller *et al.*, 2005, Ruiz-Labourdette *et al.*, 2012, García-Valdés *et al.*, 2015a). Multiple studies show that biodiversity increases community resistance and resilience to climate change effects (del Rio and Sterba, 2009, Ge *et al.*, 2011, Vallet and Pérot, 2011). For example, communities that contain species with different growth patterns may be more effective at buffering the effects of climate fluctuations on productivity, although the complementarity in water use strategies among species could also lead to increased water use and greater drought stress in the long term (Ge *et al.*, 2011, Grossiord *et al.*, 2014, Toïgo *et al.*, 2015).

Trees are organisms especially vulnerable to the stress caused by fluctuations in climate, as their long longevity makes it difficult for them to adapt to environmental changes in the short-term (Lindner *et al.*, 2010). Such threat is amplified in Mediterranean areas, where drought (low water availability) and high summer temperatures are the main factors constraining tree growth (Galiano *et al.*, 2010, Linares and Tíscar, 2010). In fact, studies regarding the possible impacts of climate change identify the Mediterranean region as a hot-spot in terms of vulnerability to the predicted changes (Giorgi, 2006, Doblas-Miranda *et al.*, 2017). Climate change projections

predict an increment in annual mean temperatures of approximately 3-4°C for the European Mediterranean area by 2100 (Christensen *et al.*, 2007), with a higher increase in summer (4-5°C) than in winter (2-3°C) (Calbó *et al.*, 2012).

In addition, many Mediterranean tree populations are located at the southern edge of theirs species' distributions, which makes them more vulnerable to drought-related mortality (Sánchez-Salguero *et al.*, 2012). Thus, a regression of sub-Mediterranean tree species is expected during incoming decades, especially for those that show higher drought vulnerability (Camarero *et al.*, 2015b). Specifically, Scots pine (*Pinus sylvestris*) has been identified as one of the most vulnerable species to drought-induced dieback in Western Europe (Martínez-Vilalta and Piñol, 2002, Rigling *et al.*, 2013). It is also one of the most widely distributed species worldwide, with Mediterranean populations constituting the rear distribution edge (Hampe and Petit, 2005). Rear edge populations play a key role in genetic diversity storage and future evolutionary potential (Hampe and Petit, 2005), so further understanding of these populations' dynamics is essential.

Drought-induced mortality of Scots pine is not compensated by self-recruitment in many areas (Galiano *et al.*, 2010, Rigling *et al.*, 2013, Vilà-Cabrera *et al.*, 2013). Such low recruitment contrasts with the high regeneration that Scots pine shows under open canopies when water is available (Castro *et al.*, 2004). Moreover, increased colonization of *Quercus* species has been detected in pine forests with signs of drought-induced dieback (Galiano *et al.*, 2010, Rigling *et al.*, 2013, Vilà-Cabrera *et al.*, 2013), where open gaps left by adult tree mortality create a more xeric environment (cf. Suarez and Kitzberger, 2008). Legacies of previous land use and forest management practices could also explain increased oak colonization (Rigling *et al.*, 2013, Vayreda *et al.*, 2016). In the past, intensive forest pasture, firewood extraction and litter raking

apparently prevented the regeneration of deciduous trees (Gimmi *et al.*, 2010). Thus, the abandonment of these practices has had a positive effect on oak species regeneration at the expense of pine species (Rigling *et al.*, 2013, Vayreda *et al.*, 2016), supporting the hypothesis that current tree species distributions are far from equilibrium with current climate (García-Valdés *et al.*, 2013). This fact, together with broadleaf species' greater capacity to respond to disturbances and their higher competitive ability (Vayreda *et al.*, 2016), may be causing *Pinus sylvestris* to be replaced by oaks in many European forests (Galiano *et al.*, 2010, Rigling *et al.*, 2013, Vilà-Cabrera *et al.*, 2013). However, it is unclear whether this trend will continue under a warmer and drier climate, and what will be the consequences of this current vegetation shift in terms of future forest functioning.

Due to the inherent difficulties associated to long-term experimental studies with trees, Forest Succession Models (FSMs) have been proved as valuable tools to study forest behavior under climate change in temperate forests (Rasche *et al.*, 2011). Such models simulate individual trees (or cohorts) establishment, growth and mortality, as well as population dynamics, typically accounting for climatic effects and for competition for light (Bugmann, 1996). In this study, we used the previously validated FSM ForClim v2.9.6 (Bugmann, 1996, Didion et al., 2009, Rasche et al., 2011) to assess the effects of climate change on Mediterranean *Pinus sylvestris* and *Quercus humilis* populations in Catalonia (North-Eastern Iberian Peninsula). These two species are widespread in the Mediterranean basin and frequently coexist. Specifically, we address the following questions: (1) Are these two species going to be differentially affected by climate change? and what will be the implications for succession dynamics in Mediterranean forests? (2) How is this going to affect the forest community's properties and functions such as wood biomass and productivity? (3) Are the expected

changes different for areas currently dominated by either species (monospecific stands) relative to areas where the two species currently coexist (mixed stands)?

Materials and methods

Study area

Our study area is Catalonia, located in NE Spain. This region presents a high altitudinal gradient, ranging from sea level to more than 3000 m a.s.l. in the Pyrenees. Such geographic heterogeneity results in high climatic variability. Mean annual temperature ranges from 1°C in the alpine area (NW) to 17°C in the Southern areas, and annual precipitation values range from 350 mm to 1500 mm, increasing with latitude (Ninyerola *et al.*, 2000). Catalonia has 38% of its total area covered by forests (1.2 million ha), which are dominated, in terms of distribution area, by *Pinus halepensis*, *Quercus ilex* and *Pinus sylvestris* (Gracia *et al.*, 2000-2004).

We focused our study on *Pinus sylvestris* L. and *Quercus humilis* Mill. (including *Q. cerrioides;* Willk. & Costa) forests. These two species are representative of Mediterranean mountain forests, and cover 220,000 and 62,000 ha, respectively, in Catalonia (Gracia *et al.*, 2000-2004). Populations of *Pinus sylvestris* in the study area are in the southern end of its distribution and have been shown to be highly vulnerable to climate change-type droughts (Martínez-Vilalta and Piñol, 2002; Heres *et al.*, 2012; Vilà-Cabrera *et al.*, 2013). Since both species frequently coexist in transition areas, the replacement of *Pinus sylvestris* by *Quercus humilis* appears as a likely vegetation shift (Galiano *et al.* 2010; Rigling *et al.* 2013).

We used the Ecological and Forest Inventory of Catalonia (IEFC; Gracia *et al.* 2000-2004), with a total of 10664 forest plots, and selected plots where the combined basal area of the two study species was > 80% of the total plot basal area. To ensure that

very open forests were not included we selected plots that had more than 4 m^2/ha of total basal area. Plots that showed signs of forest management or recent fires according to the information recorded during the IEFC surveys were also removed from the analyses. After the selection process, 192 plots remained suitable for our study, 99 of which corresponded to monospecific *P. sylvestris* stands, 35 to monospecific *Q. humilis* stands and 58 to mixed forests (see Table 1). Stands were considered monospecific when the dominant species had more than 80% of the total plot biomass.

Type	**Plots**	**DBH [cm]**	**LAI**	**AGB [t/ha]**	**AGP [t/ha/year]**
Pinus sylvestris	99	18 ± 5.4	1.4 ± 0.72	75 ± 51	2.4 ± 1.4
Quercus humilis	35	14 ± 4.5	1.9 ± 1.1	57 ± 43	1.6 ± 0.96
Mixed	58	16 ± 3.8	1.6 ± 0.78	64 ± 34	2.6 ± 1.2

Table 1. Summary of the selected plots characteristics. Mean (± SD) diameter at breast height (DBH), Leaf Area Index (LAI) and total above-ground biomass (AGB) and productivity (AGP) per plot type.

Forest growth simulation - ForClim

We used ForClim to simulate forest growth in every plot studied, and assess the effects of climate change on stand biomass and productivity as a function of forest composition and climatic variables. ForClim is a forest succession model that follows the standard approach of gap models (Botkin *et al.*, 1972). It simulates the cyclical succession of a pool of species depending on site-specific conditions (temperature, precipitation and competition for light) on small patches of land, while making the minimum number of ecological assumptions. Concerning tree establishment, ForClim disregards seed production, dispersal and germination, as well as seedling establishment and growth.

156 Instead, saplings are established according to minimum winter temperature, light
157 availability, deer browsing and temperature range. Tree growth is influenced by light
158 availability and soil moisture. Tree mortality is determined by each species intrinsic
159 base mortality and stress-induced mortality rates (Bugmann, 1996).

160 In our case, we included *P. sylvestris* and/or *Q. humilis* in the species pool
161 depending on the current stand composition (monospecific dominated by *P. sylvestris*,
162 monospecific dominated by *Q. humilis*, or mixed). These species were already
163 parameterized in the model (Table S1). However, the model was built around data and
164 previous results from central European forests. Such parameterization established that
165 the maximum winter temperature for *P. sylvestris* to be able to germinate was 1ºC, and
166 hence our preliminary analysis showed that this species would go extinct under climate
167 change in many stands. To determine is such parameter was realistic in our study area
168 and before accepting such extreme predictions we decided to analyze which was the
169 maximum winter temperature in which *P. sylvestris* could be found in the Iberian
170 Peninsula. To do so we analysed all the stands in which this species occurs in the 3rd
171 Spanish Forest Inventory (1997-2007 period; Villanueva, 2004). The 90th percentile of
172 the winter temperatures (maximum monthly temperature of December-February) was
173 ~5ºC. We hence decided to use this value instead of the default one (1ºC) as the minim
174 winter temperature threshold value (*WiTX*) (Table S1). No such change was required for
175 *Q. humilis*, as the ForClim parameter value is consistent with the climatic distribution of
176 the species in the Iberian Peninsula.

177 For each of the 192 plots selected, we simulated 2000 years of forest dynamics
178 starting from bare-ground conditions, and iterated this process 200 times to reduce the
179 effects of stochasticity in our results. For every simulation, we calculated the biomass
180 and productivity of the plot once it reached pseudo-equilibrium. To do so, and to reduce

181 temporal autocorrelation and avoid transient signals in the output, we averaged the last
182 1000 years of the simulation, taking information from one every 100 years.
183
184 *Climate data*
185 Climate data in each plot consisted of monthly temperature (°C) and precipitation (mm).
186 Current climate data were obtained from interpolations at 1 x 1 km resolution
187 (following Ninyerola *et al.*, 2000), from the weather station networks of the Spanish
188 Meteorological Agency (AEMET) and the Catalan Meteorological Service (SMC).
189 From the climate change data we used the ECHAM4 climatic model and A2 former
190 IPCC climate scenario as an example of a relatively extreme climate change scenario,
191 also interpolated at 1 x 1 km. For each plot, we generated two 2000-years climate series
192 using the built-in climate generator of ForClim. For the current climate scenario we
193 used data from the 1961-1990 period, and for the climate change scenario we used data
194 forecasted for the 2071-2100 period. The algorithm uses the mean and standard
195 deviation of monthly mean temperature and monthly precipitation sum, as well as the
196 cross-correlation of these two variables.
197
198 *Data analyses*
199 Biomass and productivity at the plot level were compared between the current climate
200 scenario and IEFC to test the proximity of the data simulated by the model to the reality
201 of our plots. It should be noted that the results of our simulations are based on forests
202 that have already reached pseudo-equilibrium, so substantial divergence between values
203 is expected as many forests in our study area are in early stages of succession due to
204 past management regimes and fires (García-Valdés *et al*., 2013, Vayreda *et al*., 2016).
205 Thus, this comparison is more an analysis of the maturity of the forests in our study area

than an assessment of the realism of the model as such. We also assessed the relationship between modeled values of biomass and productivity and mean values of temperature and precipitation per plot composition, using standard regression analysis.

Regarding the analysis of the effects of climate change on the studied plots, we compared the biomass and productivity obtained under the current climate scenario and a climate change scenario (ECHAM4, A2 scenario). Aiming to find the drivers behind the observed changes, we also studied the relationship between the modeled biomass and productivity values and the climatic variables (temperature and precipitation) for each plot composition using standard regression analysis.

To further understand the relationship between environmental variables and the effect of climate change we fitted a linear model with the relative impact of climate change on biomass and productivity [RICC = log (value simulated under climate change / value simulated under constant climate)] as the response variables. The explanatory variables included climatic attributes (current mean annual temperature, T; and current annual precipitation, P), climate change (absolute anomaly of temperature, dT; and relative anomaly of precipitation, dP, under climate change (2071-2100) relative to current climate (1961-1990)), initial biomass and their interaction with composition (pure *P. sylvestris*, pure *Q. humilis* or mixed stands):

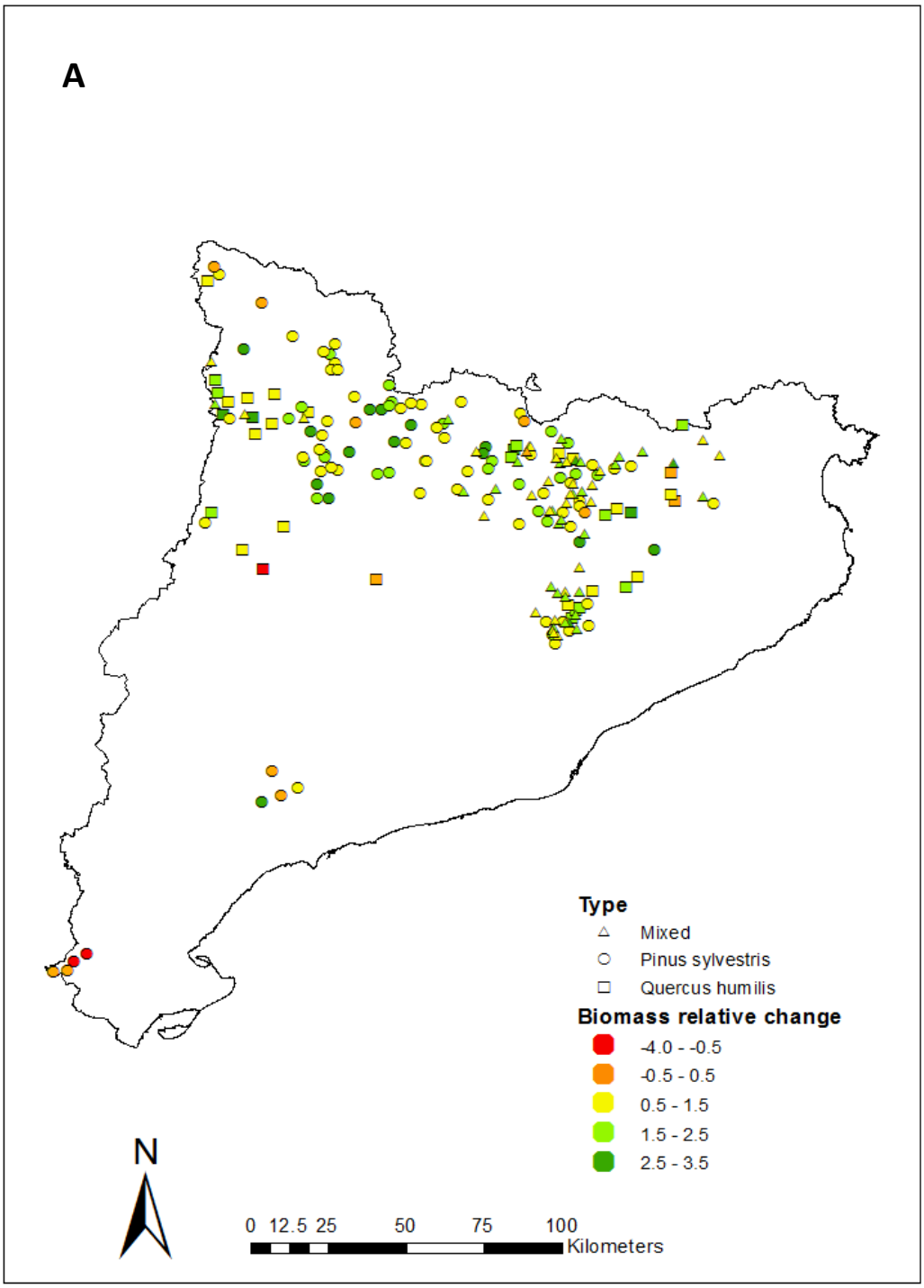
$$RICC = Composition \times (T + P + dT + dP + Biomass)$$

No significant correlation was found between the selected explanatory variables. We simplified our initial model through a stepwise procedure using a bidirectional approach (testing at every step to remove or include variables). This analysis was executed using the "stepAIC" function ("MASS" package) in R programming language.

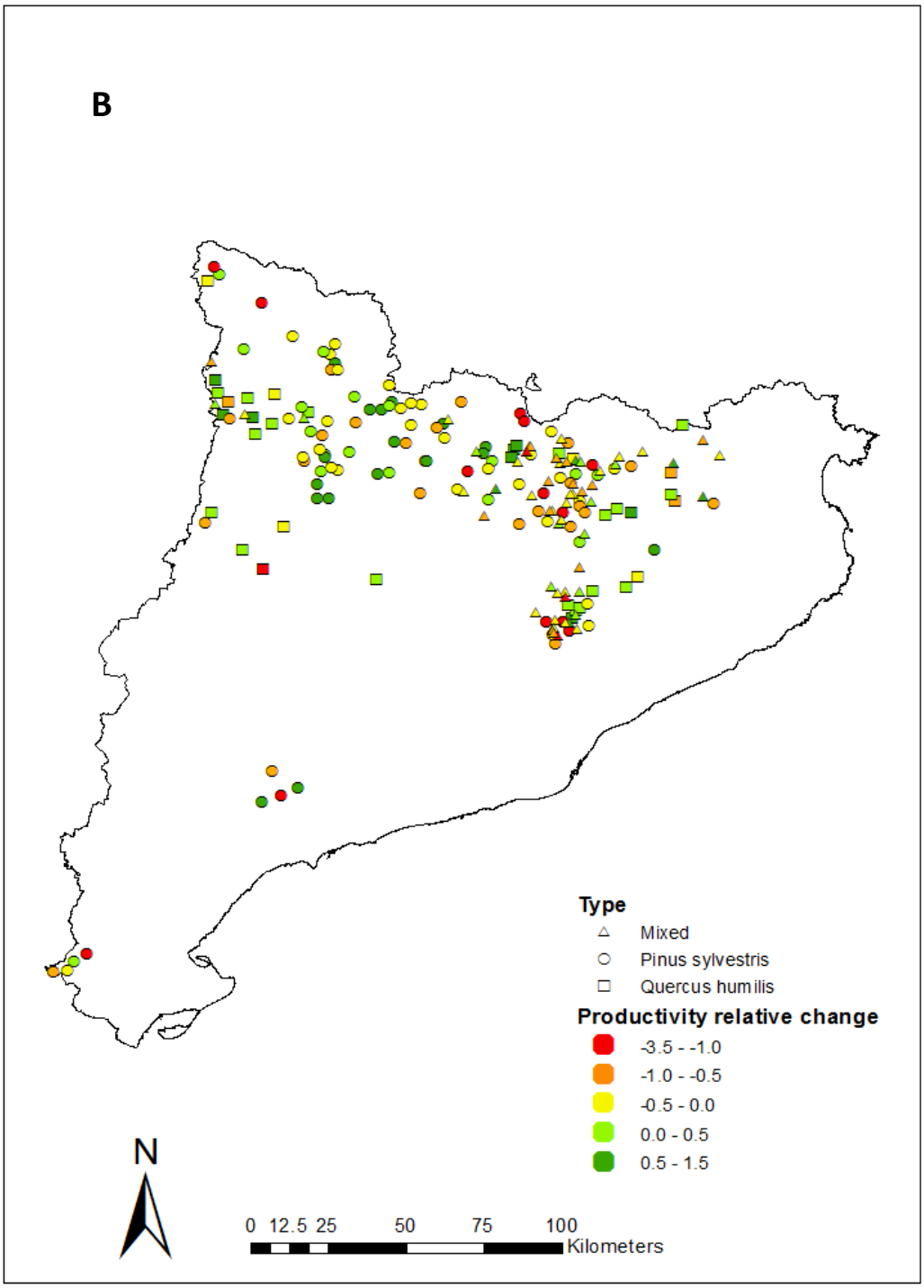
Results

Comparison between ForClim simulations and IEFC data

ForClim projected higher biomass than that measured in most IEFC surveys plots. On average, ForClim estimates were approximately three times higher (Figure 2), but in some cases they were up to 20 times higher than current values (Figure 1). As stated in the methodology, this result was expected as the analyzed plots have not likely reached a pseudo-equilibrium state. We can appreciate that the greatest ForClim overestimations are located in the central Pyrenean belt, and most of them correspond to monospecific *Pinus sylvestris* plots. There are few negative values (ForClim underestimations). The most extreme ones are *Pinus sylvestris* stands found in southern Catalonia (Ports de Beseït), and a single *Quercus humilis* stand found in the Pre-Pyrenees (Figure 1A). The results for productivity are less clear. Overall, ForClim tended to project lower values for *Pinus sylvestris* and higher values for *Quercus humilis*, compared to values measured in the IEFC survey (Figure 1B). In mixed stands ForClim projected lower total productivity, as the underestimation of *Pinus sylvestris* productivity values more than compensates the overestimation for *Quercus humilis* (Figure 2).


A
Type
Mixed
Pinus sylvestris
Quercus humilis
Biomass relative change
-4.0 - -0.5
-0.5 - 0.5
0.5 - 1.5
1.5 - 2.5
2.5 - 3.5
N
0 12.5 25 50 75 100
Kilometers

245



246

247 Figure 1. Relative difference between IEFC measurements and ForClim simulations
248 under current climate for biomass (A) and productivity (B). Relative differences were
249 calculated as log(value simulated under constant climate/IEFC measurement), so that

positive values indicate plots where ForClim predicted higher biomass or productivity than the IEFC data.

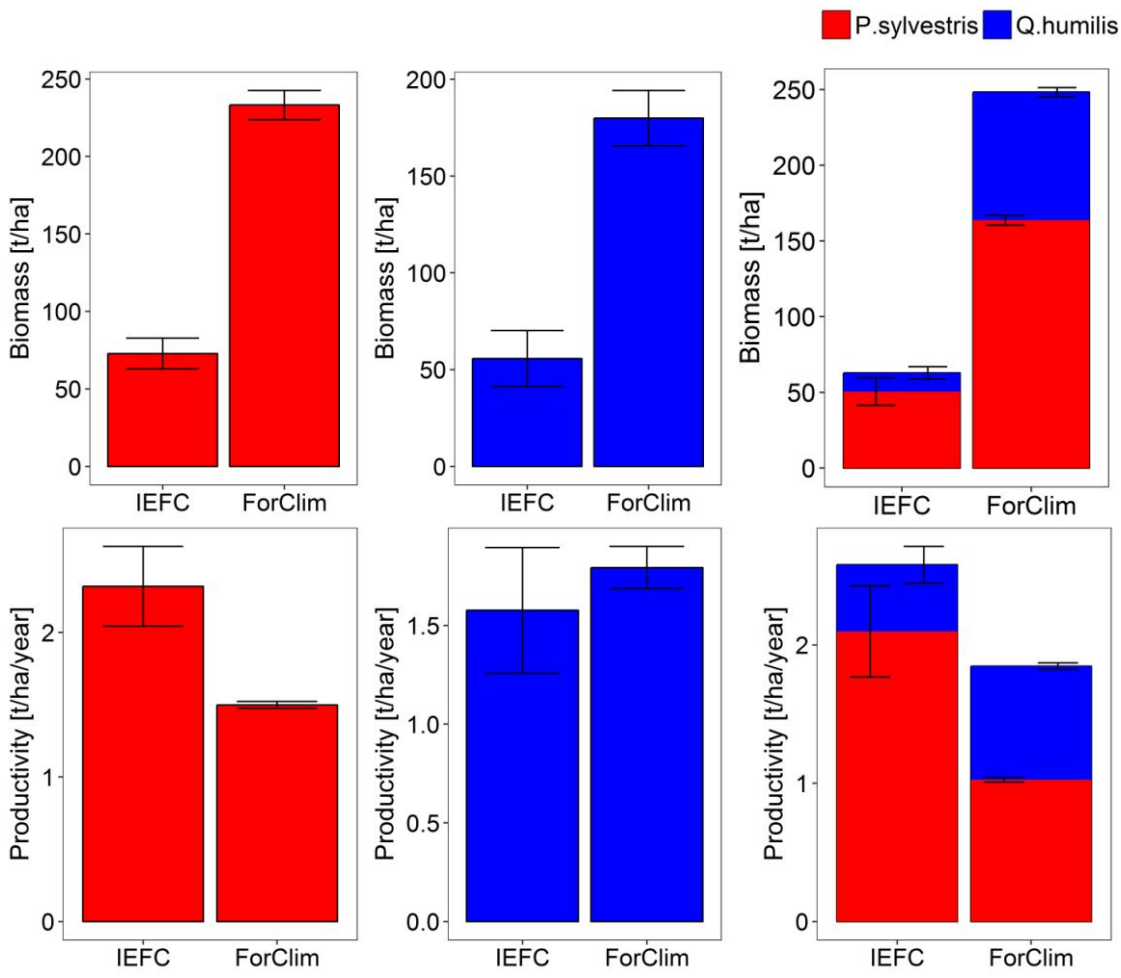
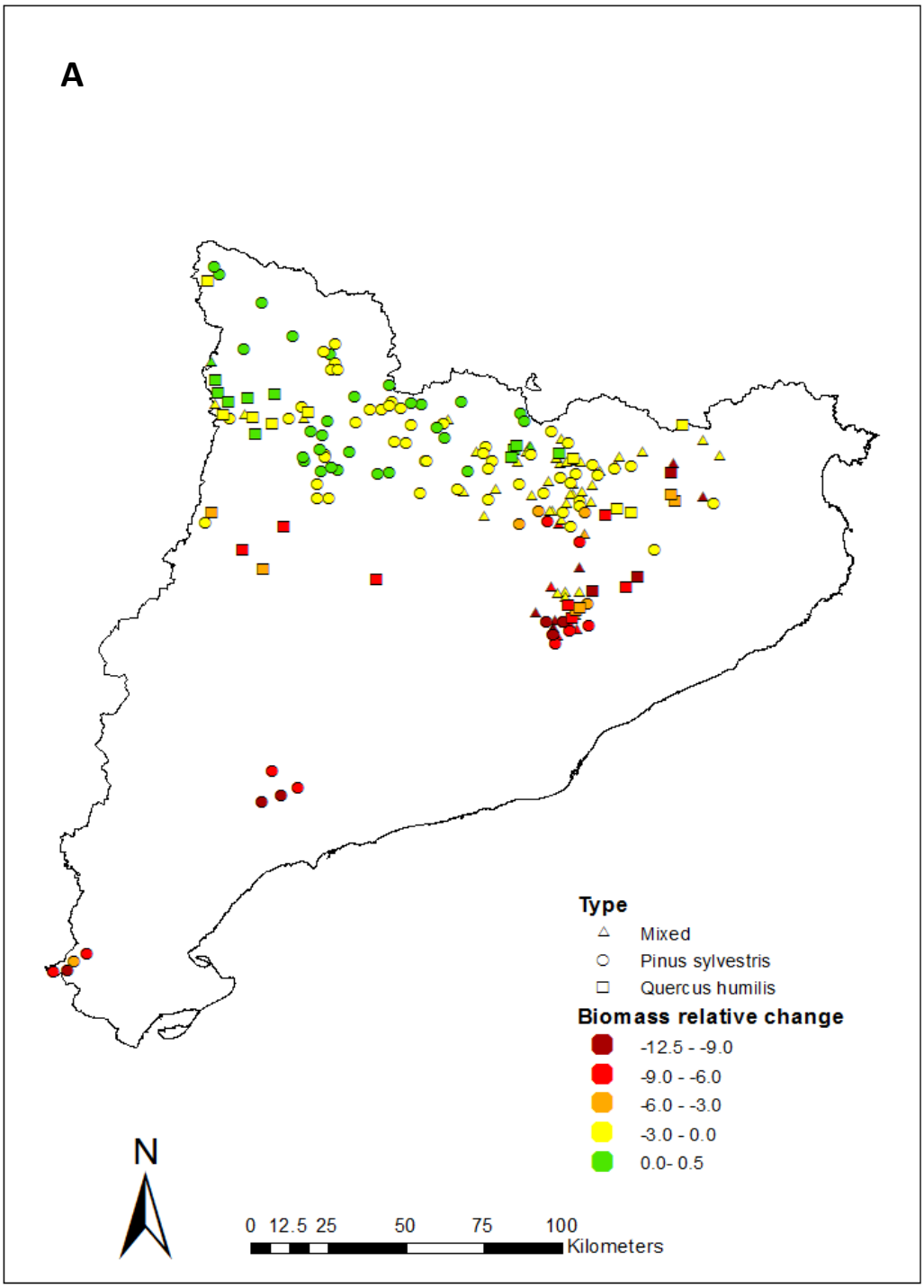


Figure 2. Mean biomass and productivity comparison between IEFC data and ForClim simulations (under current climate) per plot type (*P. sylvestris*, N=99; *Q. humilis*, N=35; and mixed stands, N=58).

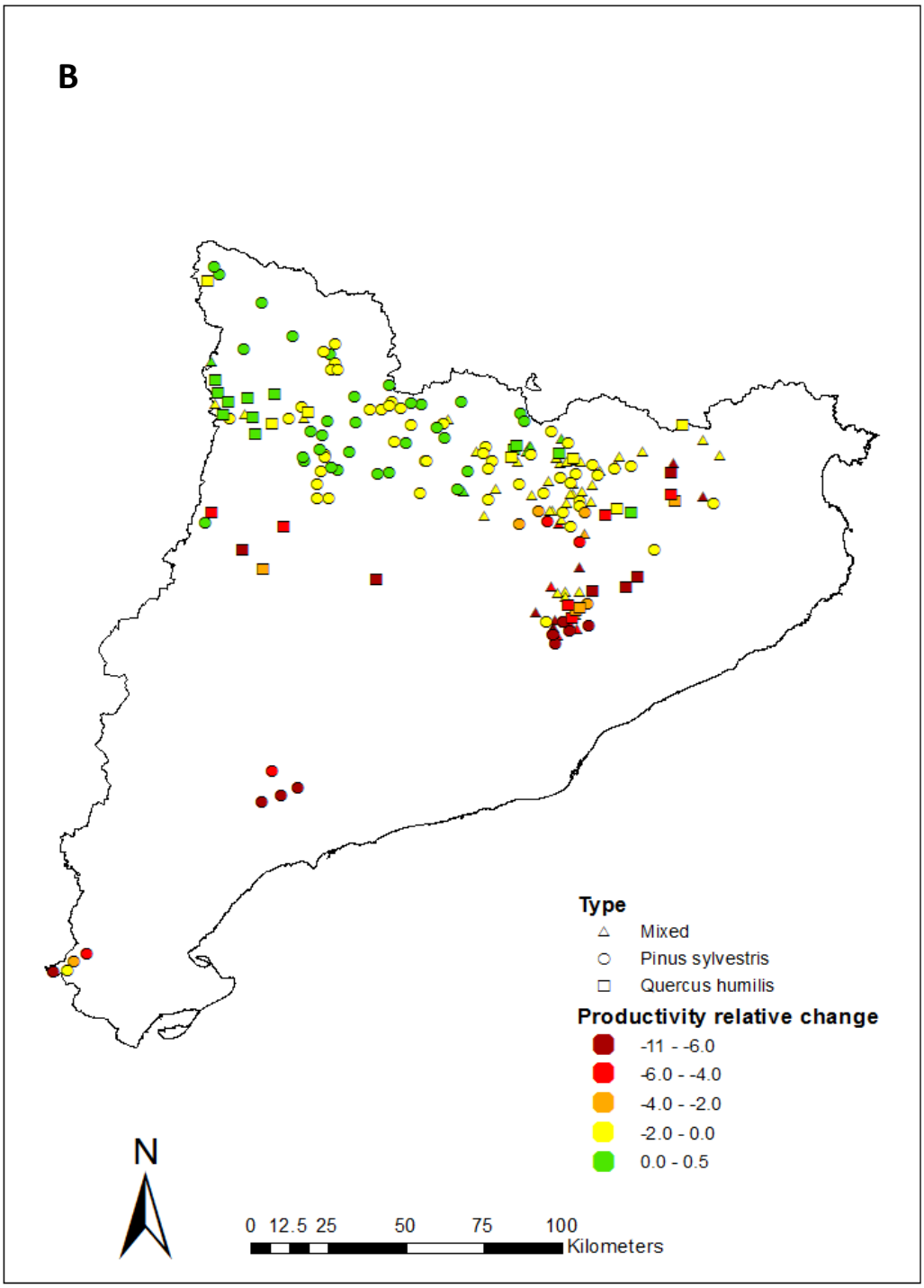
Effects of climate change

Comparing ForClim simulations from both climate scenarios we can assess how climate change may affect our study plots. Our results show a predominantly negative response in biomass and productivity. The decrease is greater in *Q. humilis* stands (45%) than in *P. sylvestris* stands (25%), with the exception of mixed stands, where the response is minimal for *Q. humilis* but there is a large decline in both biomass and productivity for

263 *P. sylvestris* (~60%, Figure 4).There is substantial variability across plots, with the
264 strongest declines for both variables found in the mountains of Southern Catalonia and
265 the Eastern end of the Pyrenees (Figure 3). Positive changes in biomass or productivity
266 are rare, and they are observed mostly in monospecific stands from the Western
267 Pyrenees (Figure 3).


A
Type
Mixed
Pinus sylvestris
Quercus humilis
Biomass relative change
-12.5 - -9.0
-9.0 - -6.0
-6.0 - -3.0
-3.0 - 0.0
0.0- 0.5
N
0 12.5 25 50 75 100
Kilometers

268



269

270 Figure 3. Relative changes in biomass (A) and productivity (B) comparing a constant

271 climate and a climate change scenario (IPCC A2). Relative changes are calculated as

log(value simulated under climate change/value simulated under constant climate). Negative values thus indicate declines under climate change.

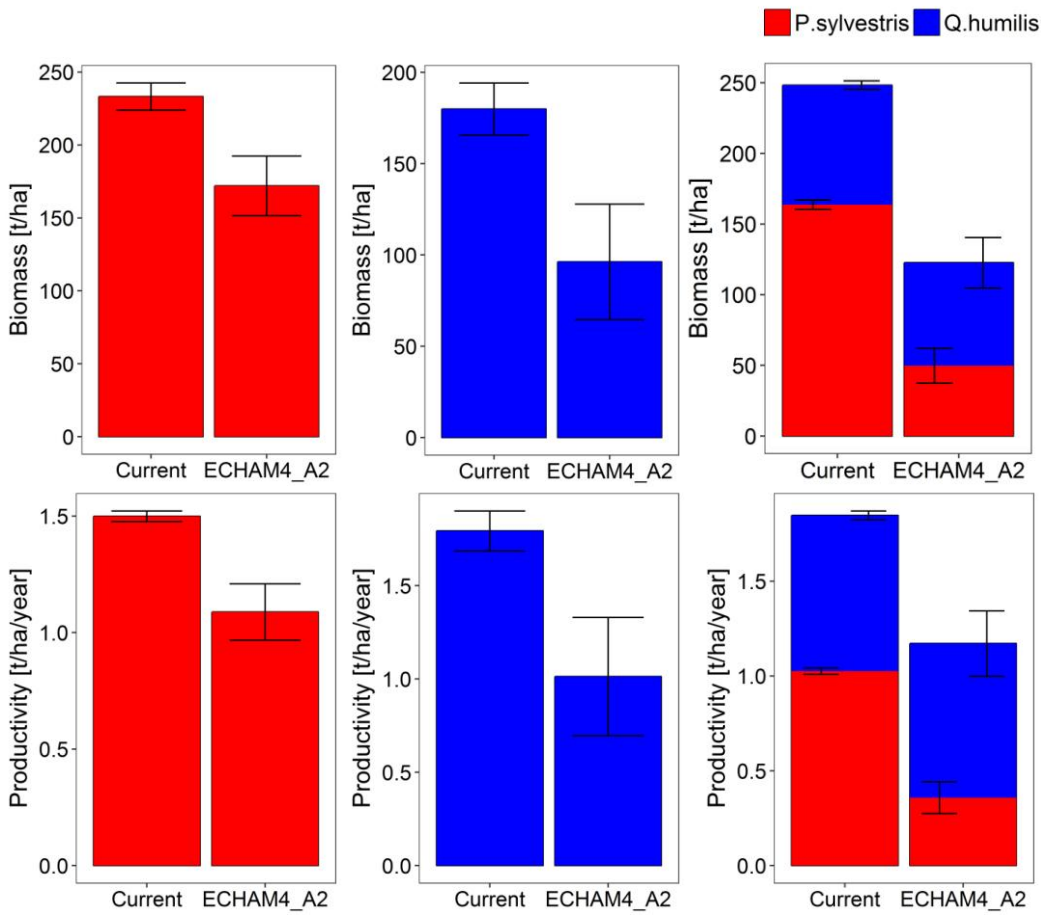


Figure 4. Mean biomass and productivity per plot type (*P. sylvestris*, N=99; *Q. humilis*, N=35; mixed stands, N=58) and climate scenario.

Drivers of climate change effects

We did not find a clear relationship between climatic variables and biomass or productivity when using measured IEFC data (Figures 5 and 6). However, when using the data obtained in ForClim simulations we found predominantly positive, saturating rainfall effects and hump-shaped temperature effects on biomass and productivity (Figures 5 and 6). These effects implied a strong negative relationship between temperature and biomass and productivity in the climate change scenario, with values

dropping drastically for temperatures > 16 ºC. Similarly, sharp declines in biomass and productivity were observed for precipitation values < 60-70 cm (Figures 5 and 6).

We used the previous results to model the relative change of biomass [log(biomass under climate change / biomass under constant climate)] as a function of climate and stand-level variables. Our final model for biomass was:

$$RICC_B = Composition + T + P + Biomass\ (IEFC) + dP + Composition{:}T$$

We observed a positive effect of precipitation and precipitation increase and a negative effect of IEFC biomass, consistent for all plot types. The negative effect of temperature was significant on all plot types, but was significantly stronger for mixed than for *P. sylvestris* plots (Table 2).

The corresponding model for relative changes in productivity [log(productivity under climate change / productivity under constant climate] was:

$$RICC_P = Composition + T + P + Biomass\ (IEFC) + dT + dP + Composition{:}dP$$

and showed negative effects of IEFC biomass and temperature and a positive effect of precipitation, consistent across all plot types. We also observed a positive effect of precipitation increase on all plot types, which was significantly stronger for mixed plots than for *P. sylvestris* stands (Table 3). Interestingly, we did not find significant effects of temperature anomaly in either model.

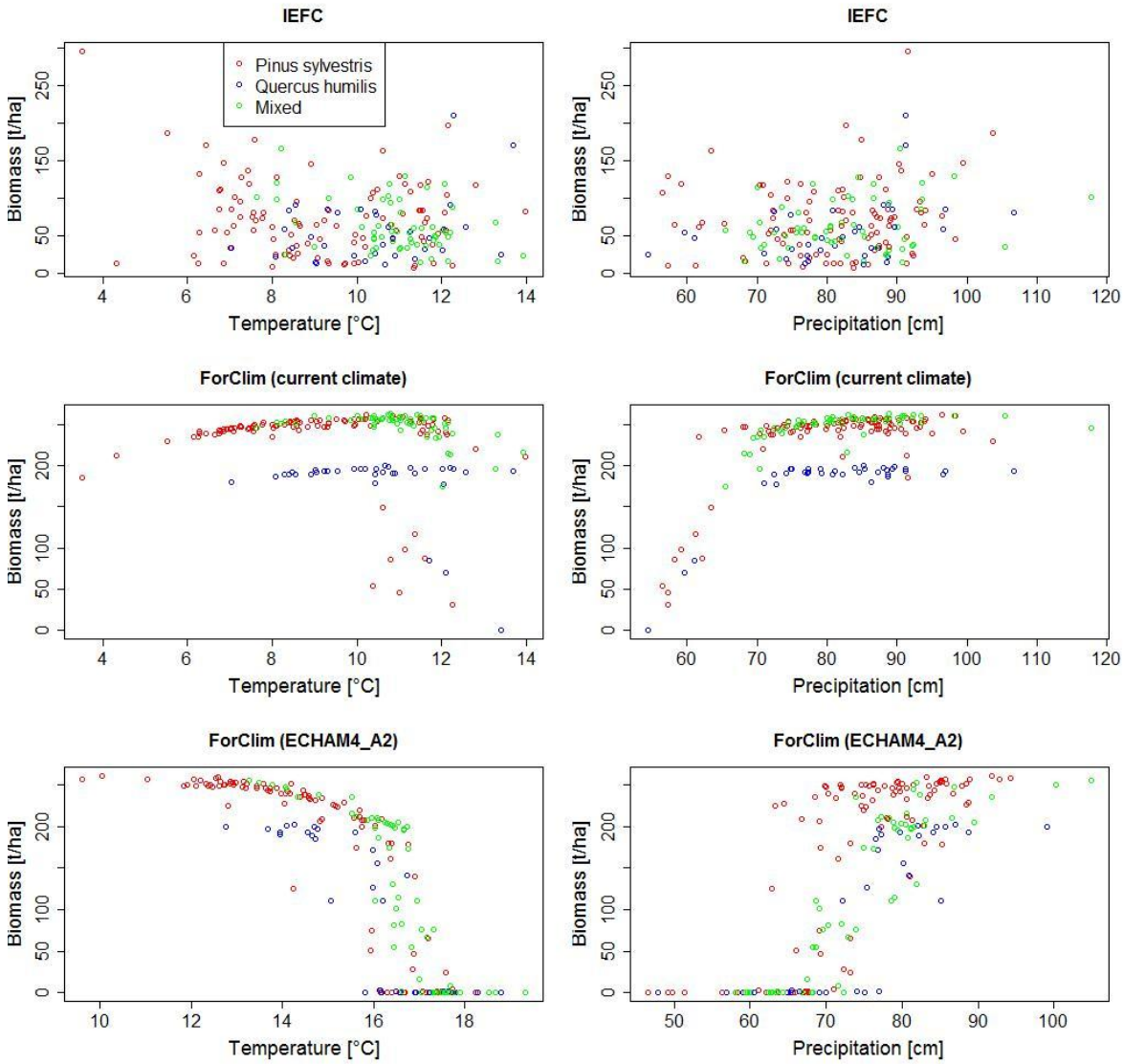
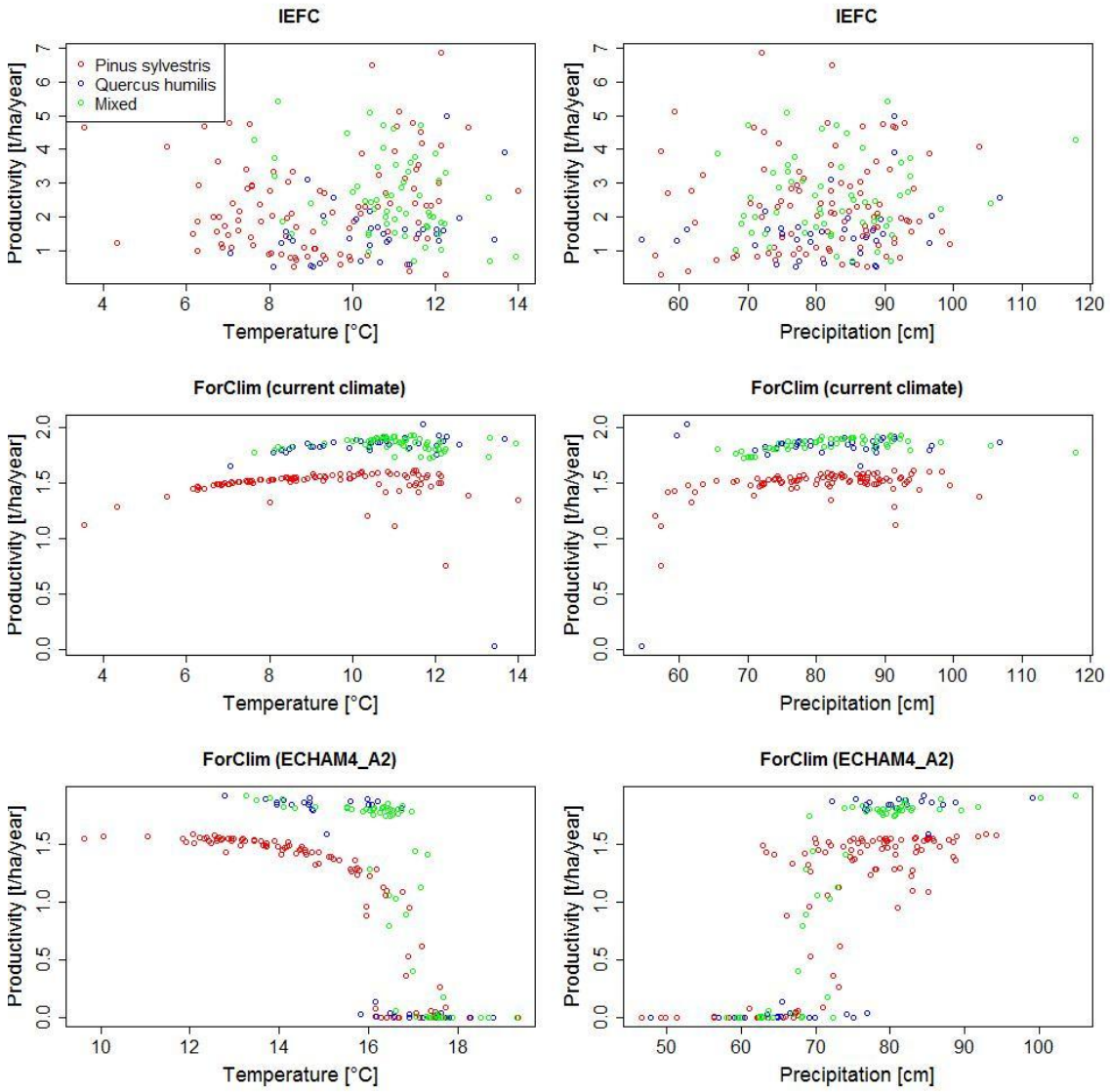


Figure 5. Relationships between plot biomass and the two climatic variables (temperature and precipitation), using IEFC data and ForClim simulations under current and climate change scenarios. Different colors indicate plot types.



307

308 Figure 6. Relationships between plot productivity and the two climatic variables
309 (temperature and precipitation), using IEFC data and ForClim simulations under current
310 and climate change scenarios. Different colors indicate plot types.

	Estimate	Std. Error	t value	Pr (>|t|)	
Intercept	-2.2136	0.2209	-10.021	< 2e-16	***
Type [Mixed]	0.5371	0.4191	1.282	0.201576	
Type [*Quercus humilis*]	-0.6284	0.4268	-1.472	0.142617	
Temperature	-1.1855	0.2217	-5.347	2.65e-07	***
Precipitation	1.6673	0.1764	9.451	<2e-16	***
IEFC biomass	-0.5292	0.1515	-3.494	0.000597	***
Precipitation increase	1.1937	0.1665	7.171	1.81e-11	***
Type [Mixed] x Temperature	-1.0748	0.4485	-2.396	0.017579	*
Type [*Quercus humilis*] x Temperature	-0.4182	0.4689	-0.892	0.373547	

311 Table 2. Summary table of the linear model for biomass (the reference level of the Type

312 variable corresponds to monospecific *Pinus sylvestris* plots).

	Estimate	Std. Error	t value	Pr (>|t|)	
Intercept	-1.6264	0.168	-9.683	< 2e-16	***
Type [Mixed]	0.3684	0.2927	1.259	0.209797	
Type [*Quercus humilis*]	-0.3912	0.317	-1.234	0.218846	
Temperature	-0.9311	0.1626	-5.726	4.27E-08	***
Precipitation	1.2768	0.1379	9.259	< 2e-16	***
IEFC biomass	-0.3875	0.1136	-3.41	0.000802	***
Temperature increase	0.2087	0.1269	1.645	1.02E-01	
Precipitation increase	0.5928	0.1606	3.691	0.000296	***
Type [Mixed] x Precipitation increase	0.5824	0.2948	1.975	0.04975	*
Type [*Quercus humilis*] x Precipitation increase	0.3815	0.2899	1.316	0.189937	

313 Table 3. Summary table of the linear model for productivity (the reference level of the

314 Type variable corresponds to monospecific *Pinus sylvestris* plots).

Discussion

Our results showed substantial negative effects of climate change on the biomass and productivity of Catalan forests dominated by the two study species, relative to the values that could be attained in the long term, if climate did not change. These projected effects are substantially different between monospecific oak or pine stands and mixed ones, with a greater negative impact on oaks in pure stands but not in mixed forests. As expected, simulations also showed that the study forests are currently far from equilibrium.

Catalan forests are far from equilibrium

Results showed that model projections using current-like climate scenario predict greater biomass levels than currently observed, likely due to the fact that the forests studied are not in equilibrium with the climate (García-Valdés *et al.*, 2013) and are in relatively early successional stages. This is probably due to a long history of management and other disturbances such as wildfires and long/intense droughts (MacDonald *et al.*, 2000, Vayreda *et al.*, 2012a, Vayreda *et al.*, 2016,). This result implies that Catalan forests could store more carbon in the future, even under the rather extreme climate scenario studied here (compare biomass according to IEFC measurements and predictions under climate change in Figures 2 and 4), albeit at a lower rate as climate gets warmer and drier (lower productivity values under climate change relative to IEFC data, cf. Figures 2 and 4). The biomass increase is appreciated in all plot types, even though the pattern is not uniform between monospecific and mixed stands. In the absence of climate change *P. sylvestris* and *Q. humilis* pure stands biomass will increase at an even rate. In mixed stands, though, we can appreciate a gradual increase of *Q. humilis* in detriment of *P. sylvestris*, but not enough to substitute

it completely at a regional level. This divergence in our results may be consequence of the assumptions of the modelling exercise we performed, as we didn't consider colonization of the other species in pure stands, thus, not allowing monospecific stands to become mixed stands.

Climate change will likely reduce the capacity of oak and pine forests to store biomass

The negative effects of climate change in terms of biomass and productivity that our model predicts for the two study species are consistent with the overwhelming majority of reports of climate change impacts on water-limited forests (Allen *et al*., 2015), and possibly reflects the fact that both species are close to their drought tolerance limits in the study area. The greater decrease in biomass and productivity of monospecific *Q. humilis* stands relative to monospecific *P. sylvestris* stands was unexpected, given the more numerous reports of drought-induced decline of the latter species in the study area (Martínez-Vilalta and Piñol, 2002, Vilà-Cabrera *et al.*, 2013). Although the two species cover similar climatic ranges in the study area, *P. sylvestris* monospecific stands reach locations with much lower temperatures (Figures 5, 6 and S1), which can partially explain their smaller negative impact under a given temperature raise.

The larger decrease in *P. sylvestris* relative to *Q. humilis* in mixed stands (Figure 4) is consistent with forest decline observations and suggests that competition may play an important role in modulating climate change-driven effects (Linares *et al.*, 2010, Vilà-Cabrera *et al.*, 2011). These findings are also consistent with previous studies reporting that climate change may favor the transition from pine forests to oak forests in some areas (Galiano *et al*., 2010, Rigling *et al*. 2013). In summary, the discrepancy between the patterns observed for monospecific versus mixed stands can be explained by how climate change may displace such stands away from the species climatic

optimum, differently depending on the current climatic distribution of each species distribution; and by the role of interspecific competition modulating species performances, in this case, beneficiating *Q. humilis* in detriment of *P. sylvestris*. However, the ultimate fate of these mixed forests remains uncertain and merits additional research.

Limitations

It is also important to consider the numerous limitations of the modeling exercise we performed. First, as mentioned before, Catalan forests are far from equilibrium with the current climate, which could lead legacies from past management to be the main driver of change during the next decades (see, for example, Vayreda *et al*., 2016). Second, ForClim was designed to work with data from central European forests, closer to the core of our study species' distribution (Bugmann, 1996), although it has been previously tested using *P. sylvestris* tree ring data in central Spain (Mina *et al.*, 2016). Third, we did not account for the effect of intra-specific variability in species traits and the corresponding changes in model parameters. This is likely important, particularly in a widely distributed species such as *P. sylvestris*, for which large structural adjustments have been reported along environmental gradients (Martínez-Vilalta *et al*., 2009). This is particularly critical because we are modeling forests at the rear edge of the distribution of the two study species, and thus the climatic conditions in our study area may be too extreme for the standard model parameterization, as seen for the parameter constraining germination with temperature, which had to be adjusted using SFI data (see Methods). Finally, regarding climate projections, we only considered one climate model and one scenario, which does not account for uncertainty in climate dynamics and may bias our results (Meehl *et al*., 2007, Hawkins and Sutton, 2009, Weaver *et al*., 2013).

In conclusion, Catalan forests are far from equilibrium, which will allow them to act as a carbon sink for years to come, even under the effects of climate change. Climate change will negatively affect both *Q. humils* and *P. sylvestris* forests, reducing their biomass and productivity, with the only exception of *Q. humilis* productivity. Such general decrease was stronger in *Q. humilis* pure stands than in *P. sylvestris* pure stands. Thus, our results do not explicitly show the expected succession from *P. sylvestris* to *Q. humils* due to exclusively climatic reasons. Contrarily, simulations for sites were both species currently coexist are consistent with this transition, and show a detriment of *P. sylvestris* in favor of *Q. humilis*. Such disparity can be attributed to the effects of interspecific competition, or simply to the intrinsic limitations of the modeling exercise we performed. Overall, this study shows the difficulty of predicting the future behavior of populations at the dry edge of its species' distribution, and reinforces the idea that further research is essential to fully understand the dynamics of these communities.

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589

590 # Supporting Information

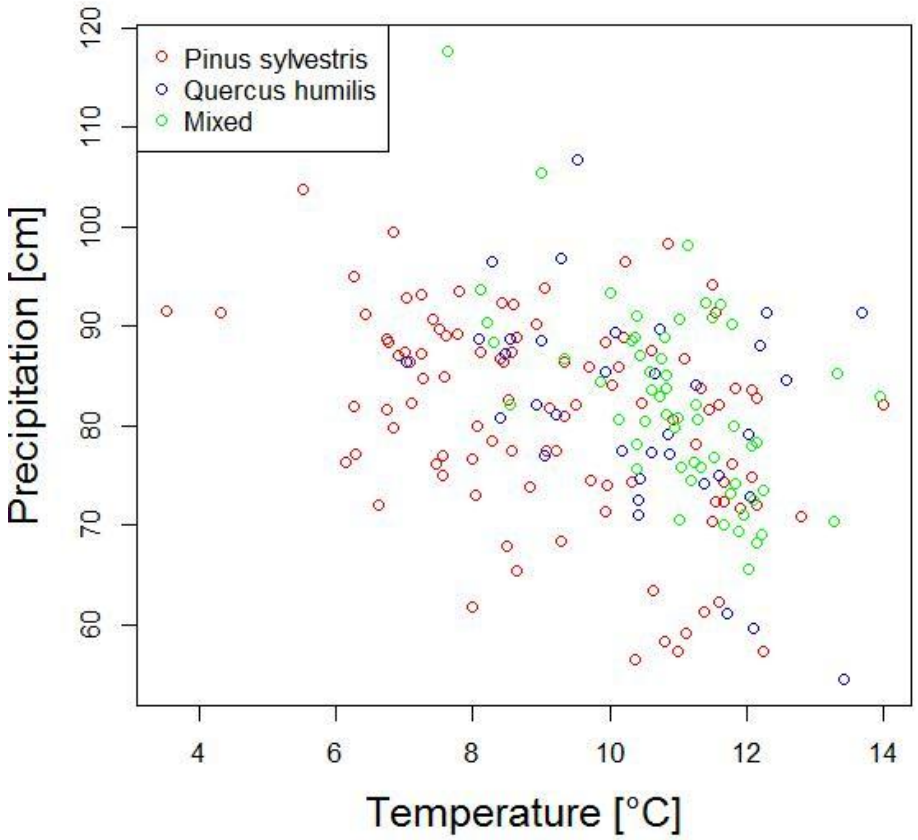
591 Table S1. Studied species and their associated parameters in ForClim.

Species	*Pinus sylvestris*	*Quercus humilis*
Type	E4	D3
S	111	50
HMax	45	25
AMax	760	500
G	119	148
DDMin	610	1011
WiTN	-100	-100
WiTX	1	9
DrTol	0.37	0.33
NTol	1	2
Brow	3	4
Ly	0.3	0.3
La	9	7
LQ	3	2
ImmT	-12000	-12000
Age Maturity reproduction	40	40

592

593 Figure S1. Current climate space (mean annual temperature and precipitation) occupied

594 by the study plots. Different colors indicate plot type.



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